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A plant root system architectural taxonomy: A framework for root nomenclature

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Abstract
Research into root system morphology over the last two centuries has developed a diverse set of terminologies that are difficult to apply consistently across species and research specialties. In response to a need for better communication, a workshop held by the International Society for Root Research established some nomenclature standards for root research. These standards and their justification are presented in this study. A framework for a root system architectural taxonomy is created by defining four main classes of root: the tap root, that is, the first root to emerge from the seed; lateral roots, which are branches of other roots; shoot-borne roots, which arise from shoot tissues; and basal roots, which develop from the hypocotyl, that is, the organ which is between the base of the shoot and the base of the tap root. It is concluded that adherence to the presented taxonomy will reduce confusion and eliminate some of the current confounding of results.

Keywords: *Nomenclature, tap root, basal root, shoot-borne root, lateral root*

Introduction

Ongoing and future research on plant roots may provide high-impact solutions to current and future food scarcities: such as a second green revolution (Lynch 2007) or a blue revolution (Finkel 2009). Both of these positive scenarios rely on the concept that plant roots have been inadequately exploited because they comprise the hidden half of plants, that is, are not normally visible and are relatively difficult to study (see discussions within Waisel et al. 2002). Although there is extensive ongoing research on roots, this research is commonly fragmented into model plant research or commodity/species efforts. This has led to a lack of cross-communication and to a diverse nomenclature to describe the research results. In order to achieve the above "revolutions", rhizobotanists and rhizogeneticists will need to use a common vocabulary to avoid duplication, confusion, misinterpretation and errors. The following discussion presents (a) an overview of the need for a common nomenclature, (b) a recommended framework for plant root system taxonomy, and (c) some genetic and functional support for this root system taxonomy.

Overview

Because roots normally reside in the soil, they cannot easily be observed except through some form of disturbance or severe alteration to their environment (Böhm 1979; Smit et al. 2000). It is difficult, therefore, to follow up the developmental ontogeny of a single root system with existing technology. An exception is research in the "Sarah Racine Root Research Laboratory", which uses large-scale aeroponic culture techniques to allow visual and physical access to roots of even grown-up trees (Waisel 2002). Because of soil opacity, much of recent research on roots has been restricted to seedlings and young plants or to very small plants such as *Arabidopsis thaliana* (L.) Heynh. With this wealth of knowledge based on immature root systems, it is convenient (but inaccurate) to assume that the conclusions are translatable to mature root systems and to all other plant species. In addition, knowledge

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of the developmental sequence from seedling to maturity is required for accurate interpretation of causal relationships.

Root research was practiced long before Darwin postulated that the root tip was the plant "brain" (see Trewavas 2007; Barlow 2009). Throughout such research history, each scientist, working with his own species and growing conditions, has developed his own descriptive terminology for the plant parts he has investigated. Classically, only three types of roots were recognized, that is, the tap root, lateral roots and adventitious roots (Esau 1965; Fahn 1982). Most researchers simply assumed that root systems were homorhizic, that is, all roots are equivalent in morphology and function. This gave rise to topological classification systems (Fitter 2002) to assess the functionality of different root distributions. Discrepancies began to arise when mutations of roots of tomato (*Solanum lycopersicum* L., Zobel 1975) and corn (*Zea mays* L., Hochholdinger et al. 2004) were genetically analysed and the functionality of different root types was compared (Waisel & Eshel 2002, 2009). Evidence that there are significant genetic and functional differences between basal, seminal and shoot-borne/nodal roots has been accumulating (Zobel 1975; Hetz et al. 1996; Waisel & Eshel 2002, 2009; Hochholdinger et al. 2004). In light of the increasing use of plant ontologies (Blake 2004), these differences need to be formalized for accurate inclusion in the respective ontologies.

To account for the improving definition of root system architecture, and provide a framework to work from, the International Society for Root Research (ISRR) held a workshop that recommended the use of a standardized root nomenclature. The recommendations were approved by the general assembly and this is an official publication of that nomenclature with additional comments to clarify some of the architectural and anatomical aspects. A slightly modified version of the approved architectural taxonomy was published by Zobel (1989) and Gregory (2006).

The workshop report

Root measurements

Root measurements and nomenclature have to use SI units.

- *Biomass*. It was felt that those interested in roots should use the root/shoot ratio, as opposed to the shoot/root ratio that one can find in various textbooks. There was some discussion of the lack of the real meaning of these ratios and it was suggested that an allometric relationship be used (i.e. the log of root weight plotted against the log of total plant weight or against the shoot weight).
- *Diameters*. On the subject of root diameters, the consensus was to use Böhm's (1979) list of diameter classes (Table I) as the most appropriate nomenclature for the present, but with some additions.

Root system morphological taxonomy

Four root classes based on the site of origin were proposed:

(1) *Tap root*. The first root to emerge from the seed is to be called the "tap root" (Esau 1965). This term to be applied also to the radicle or its replacement root after damage to the original tap root.
(2) *Lateral roots*. The term "lateral root" was accepted for any root branching from another root (Esau 1965). To assist in describing the precise relationship of the lateral roots, branches of the three primary (axial) classes of roots, should be called "first-order laterals". Branches from these first-order laterals are then second-order and so on. The full description of a specific second-order lateral would be a "second-order lateral of the tap root", or "second-order lateral of the basal root" and so on.
(3) *Shoot-borne roots*. The term "shoot-borne root" (Sprossbürtige Wurzeln) has been repeatedly used in the literature (Esau 1965).
(4) *Basal roots*. The term "basal root" was chosen for roots originating from the hypocotyl (sometimes called mesocotyl), which is the organ between the base of the shoot and the base of the tap root (Weinhold 1967). Except for the radicle (the tap root), the seminal roots of monocots are basal roots. There is no known published (nomenclatural) equivalent to seminal roots for dicotyledonous plants.

Figure 1 shows three of these root classes on both a dicotyledonous plant (soybean) grown aeroponically and a monocotyledonous plant (wheat) grown hydroponically. Note the structural similarities.

Table I. Böhm's root classification by diameter (mm).

Very fine	Fine	Small	Medium	Large	Very large
$x < 0.5$	$0.5 < x < 2.0$	$2 < x < 5$	$5 < x < 10$	$10 < x < 20$	$x > 20$

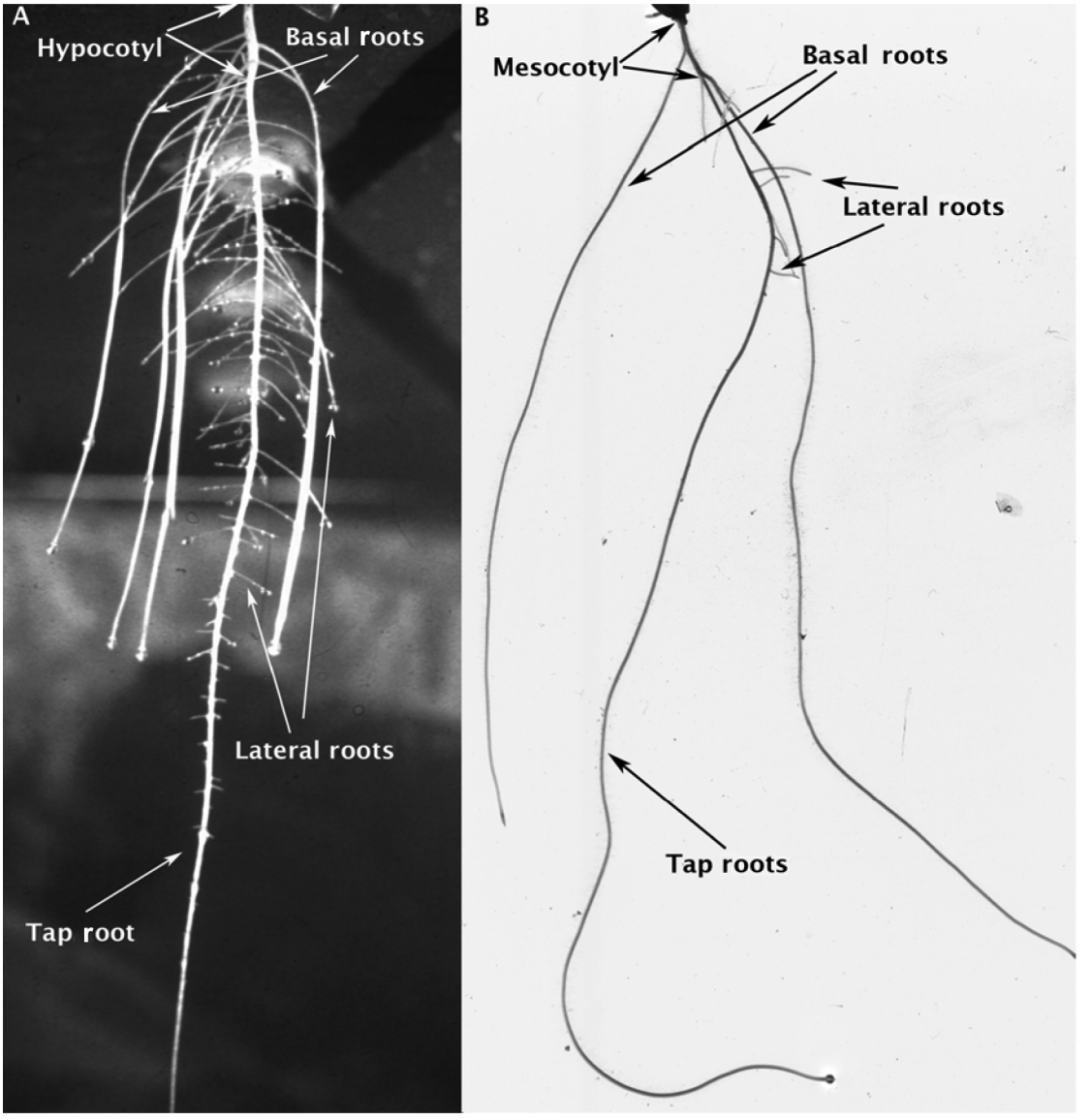

Figure 1. Roots of two plants showing the three classes of root found in seedlings: tap root, basal roots and lateral roots. (A) A soybean seedling grown in aeroponics, and (B) a wheat seedling grown in hydroponics. Both plants show a distinct hypocotyl.

Figure 2 shows shoot-borne roots and their laterals of a perennial ryegrass plant excavated from the soil.

Discussion

The approved nomenclature for root classes assumes that plant axes have a basic structure made up of roots, hypocotyl and shoots. The resulting classification system, or taxonomy, is based on easy-to-detect visual characteristics rather than on anatomical or functional characteristics. This allows classification without the need to determine specific anatomical, functional or developmental processes. This taxonomy provides a framework within which further descriptions and classifications can be added as needed. For example, "determinate lateral" (i.e. lateral roots that abort their apex after growing a centimetre or so (see McCully 1987)) is one such sub-class that has been discussed in the literature. The removal of the term "adventitious" from the main taxonomy should reduce future confounding and confusing descriptions and allow ease of comparison of results across experiments and species.

Detailed plant ontologies are in their infancy, but are being merged with species-specific ontologies (database: Gramene 2009 – grasses, TAIR 2009 – *Arabidopsis*, MaizeGDB 2009 – corn, see reference list for websites) into a single plant ontology (Plant Ontology Consortium 2009) where researchers can search for appropriate terms and report molecular, genetic and anatomical characterizations. A core taxonomy will assist in the definition

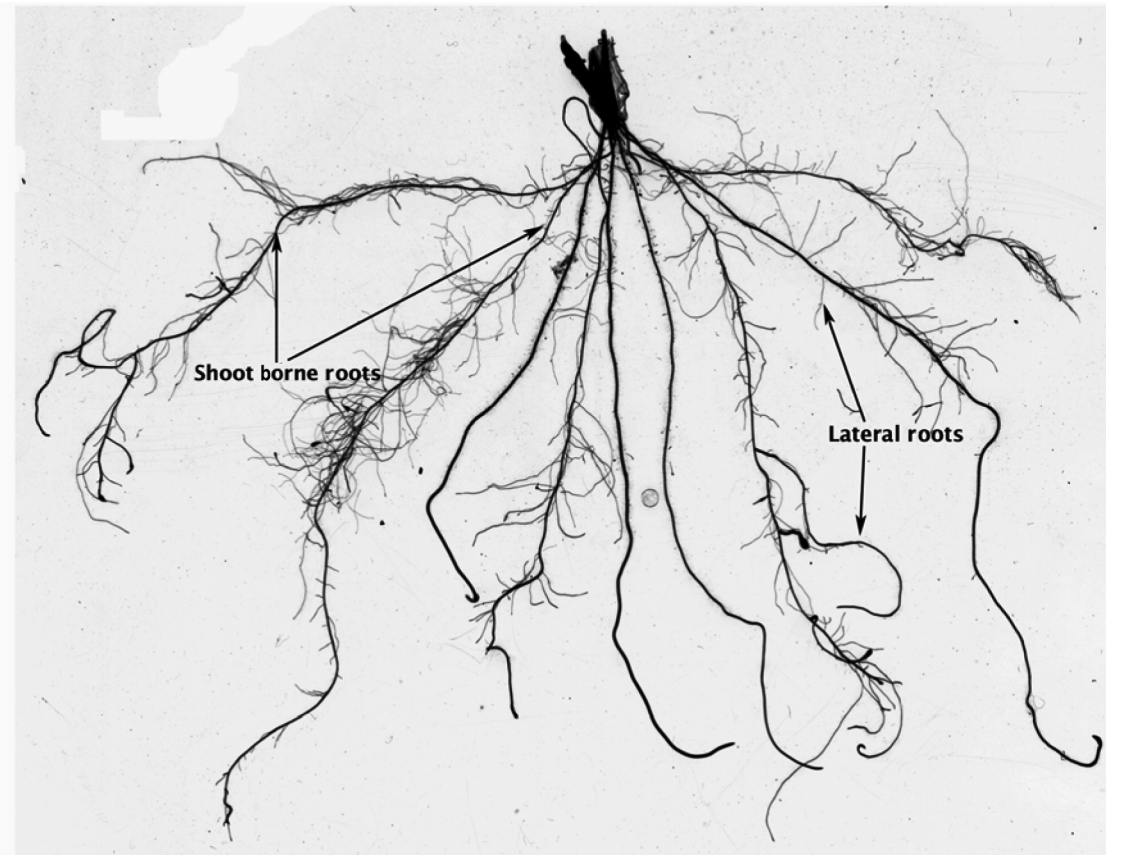

Figure 2. Perennial ryegrass (*Lolium perenne* L.) plant (transplanted from a clone) grown in soil, demonstrating shoot-borne roots and lateral roots.

of species-independent root-related ontology terms and reduce the level of confusion and the potential for confounding of results.

Evidence for structural differentiation of root classes

The derivation of tap and lateral roots is straightforward, historically, morphologically and anatomically. The only qualification is the use of the synonyms of tap root, namely, primary root, radicle and primary seminal root, in different plant species and therefore in their ontologies. Shoot-borne roots are equally clear, but their relationship to basal roots needs clarification. The term "basal root" was chosen (Zobel 1975) to represent roots that arise from the hypocotyl, a plant organ that is immediately basal to (i.e. below the base of) the plant shoot and abasal to (i.e. above the base of) the tap root. The hypocotyl (sometimes referred to as mesocotyl in the grasses – see Esau 1965) is exceedingly short in many species, resulting in the assumption that the roots arising from that region are coming from the boundary between the shoot and the tap root – therefore termed "boundary roots" or "Grenzwurzeln". According to Weinhold (1967), there has been disagreement about Grenzwurzeln since, at least, the second half of the nineteenth century. In a detailed study, with both monocots and eudicots, Weinhold (1967) demonstrated that both types had roots initiating from the pericycle in that portion of the hypocotyl which still has a stele that is anatomically typical of the tap root. It was also demonstrated that new initiations of such roots occur acropetally towards the shoot rather than downwards toward the tap root apex. The anatomy of the hypocotyl has mixed root and shoot characteristics, going from purely root anatomy at the junction with the tap root to purely shoot anatomy at the junction with the shoot (Esau 1965; Fahn 1982). The demonstration of a unique pattern of root development in this organ and the functional and genetic characterization of basal roots described next argue for the uniqueness of the hypocotyl as a distinct plant organ at the level of the main axis of the plant, for example, shoot versus hypocotyl versus tap root.

In plants with very short hypocotyls, the acropetal initiation of basal roots provides an additional aid in the determination of basal versus lateral root. In many plants, the depth of planting and the lack of light determine the length of the hypocotyl and thus the ease of observing the site of basal root initiation. Also, there is usually a significant temporal gap

between the initiation of basal roots and that of the first lateral root off the tap root (Weinhold 1967).

Genetic definition of root classes

Three plant species make up the bulk of the research on genetically based definition of root classes: tomato (*Solanum lycopersicum* L., see Zobel 1992), maize (*Zea mays* L., see Hochholdinger et al. 2004) and *Arabidopsis* (*Arabidopsis thaliana* L. Heynh.). The first genetic description of basal roots was by Zobel (1975), in which a lateral rootless tomato root mutant (*dgt*) was hybridized with a shoot-borne rootless mutant (*ro*). Roughly one-sixteenth (6.25%) of the F_2 plants were without both lateral and shoot-borne roots. These plants, however, had roots emerging from the hypocotyl. This genetically defined differences between lateral, basal and shoot-borne roots. Additional genetic support comes from Hetz et al. (1996) with the maize root mutant *rtcs*. In this mutant, both shoot-borne and basal roots are missing. Applications of naphthalene acetic acid (NAA), however, stimulate the development of basal roots on the hypocotyls but not of shoot-borne roots (Hetz et al. 1996; Hochholdinger 2004). In *Arabidopsis*, mutants have also been used to demonstrate the independent genetic control of basal root initiation relative to that of lateral roots (Boerjan et al. 1995; Sorin et al. 2005).

Functional definition of root classes

Waisel and Eshel (1992) demonstrated differential nutrient uptake between tap and lateral roots and demonstrated different patterns along the roots. Zobel et al. (1992), using ion-specific microelectrodes, demonstrated similar functional differences between tap, lateral and basal roots in both temporal uptake timing and patterns along the root. Bushamuka and Zobel (1998a) demonstrated this in nominally aluminum-tolerant cultivars of maize and soybean. Each cultivar and species had different sensitivities to aluminium in relation to the tap root, the basal roots and the lateral roots. Different soybean and maize cultivars also have different patterns regarding which class of root is able to penetrate a compacted layer of soil (Bushamuka & Zobel 1998b), thus extending the functional differentiation to the physical environment. Ofek et al. (2007) demonstrated that in aeroponics, lateral roots and tap roots support different microbial populations, presumably through differences in exudation. Zobel (unpublished work) has confirmed this differential support of microbial populations with shoot-borne versus lateral roots of perennial ryegrass grown in the soil.

Conclusion

A plant root system is composed of four basic classes of roots, identified by the site of their origin on the plant: tap (embryonic first root), lateral (branch of another root), basal (hypocotyl-borne root) and shoot-borne roots. These classes are also genetically and functionally distinct from each other. To reduce the confounding of research results, researchers are admonished to treat these different classes of root as separate entities when they design experiments and analyses.

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